TWO NEW EARLY MIOCENE THYLACINES FROM RIVERSLEIGH, NORTHWESTERN QUEENSLAND

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Thylacines, *Wabulacinus ridei* gen. et sp. nov.and *Ngamalacinus timmulvaneyi* gen. et sp. nov., are described from the early Miocene of Riversleigh, northwestern Queensland. Both show carnivorous adaptation intermediate between that of the plesiomorphic *Nimbacinus dicksoni* and derived *Thylacinus*. The family concept is revised to include these new taxa. All known thylacinid genera occur in late Oligocene to middle Miocene Riversleigh faunas and some may have overlapped in time followed by a decline in family diversity since the Miocene. □ *Thylacine, marsupial, carnivore, Miocene, Riversleigh, Queensland.*

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The Thylacinidae consists of three species of *Thylacinus* (*T. cynocephalus* Harris, 1808, *T. potens* Woodburne, 1967 and *T. macknessi* Muirhead, 1992) and the monotypic *Nimbacinus dicksoni* Muirhead & Archer, 1990 from the late Oligocene to middle Miocene of Queensland and the Northern Territory (Muirhead & Archer, 1990). It is the oldest and most primitive thylacinid, more closely resembling dasyurids in many plesiomorphic features. *Thylacinus potens* from the late Miocene Alcoota Local Fauna (Woodburne, 1967) is considered (Archer, 1982) the sister species of modern *T. cynocephalus* and is almost as specialised. *Thylacinus macknessi*, from early to middle Miocene Riversleigh faunas, is also a highly specialised thylacine. Because it retains some plesiomorphic features, it is considered to be the sister species to the *T. potens* -*T. cynocephalus* clade (Muirhead, 1992). Two new early Miocene thylacinids from Riversleigh are described here. In many features they provide a continuum in morphological change from the plesiomorphic dentition of *N. dicksoni* to that of specialised *Thylacinus*. Dental nomenclature follows Flower (1869) and Luckett (1993) where the adult dentition includes P1-3 and M1-4. Taxonomic nomenclature follows Muirhead & Archer (1990). Material is housed in the Queensland Museum (QMF) or Northern Territory Museum.

SYSTEMATICS

Order DASYUROMORPHIA (Gill, 1872)
Superfamily DASYUROIDEA (Goldfuss, 1820)
Family THYLACINIDAE (Bonaparte, 1838)

Wabulacinus gen. nov.

TYPE SPECIES. *Wabulacinus ridei* gen. et sp. nov.

ETYMOLOGY. Wanyii *Wabula*, long ago; Greek *kynos*, dog. Masculine.

DIAGNOSIS. Infraorbital foramen surrounded wholly by the maxillary and positioned low and anterior to M^1; centrocrista and preparacrista parallel, forming continuous straight line on M^1; entoconid absent (on M_3); hypoconulid enlarged (on M_3).

COMPARISON. *Wabulacinus* differ from *N. dicksoni* by larger size, lack of stylar cusps B and D on M^1, lack of stylar cusp B on M^2 and the minute size of St D on this tooth, the straight or almost straight centrocrista on M^1 and M^2, anterior cingulum of M^1 has no notch for placement of preceding premolar, the anterior root of M^1 lies directly under the cingulum, the anterior width of the upper molar crowns are less than that of the buccal lengths, wider angle of crests at the paracone and metacone, extreme reduction of the talonid basin and protocone, particularly on M^1 with concurrent loss of metaconules on this tooth, extreme reduction in size of the metaconid, absence of entoconid, reduced talonid basin by the more lingual position of the hypoconid and lack of diastemata between P_1 and P_2.

Species of *Wabulacinus* differ from all species of *Thylacinus* in the extreme reduction of the talon and protocone on M^1, the more parallel alignment of the preparacrista with the centrocrista on M^1, a small metaconid (at least on the M_3), less elongate snout by lack of diastemata between the premolars as well as between P_1 and the canine. *Wabulacinus ridei* is similar in molar

size to *T. macknessi,* but lacks an anterior cingulum on M^1.

Wabulacinus ridei sp. nov.
(Fig. 1)

ETYMOLOGY. For David Ride for his long-term commitment to Australian vertebrate palaeontology.

MATERIAL. Holotype. QMF16851, right maxillary fragment containing M^{1-2} (Fig. 1A-C). Paratype. QMF16852 left dentary fragment with broken M_3 (Fig. 1D- F) from early Miocene (System B) Camel Sputum Site, Godthelp Hill, Riversleigh.

DIAGNOSIS. As for genus.

DESCRIPTION. Maxilla partly preserved. Infraorbital foramen enclosed within the body of maxilla, above the posterior alveolus of P^3.

Buccal crown of M^1 length exceeds anterior width. Metacone largest cusp followed by paracone, protocone and St E. No other cusps. Postmetacrista longest crest, curving buccally at the posterior end. Preparacrista orientated almost parallel to the tooth row, terminating at the anterior tip of the crown. Premetacrista and postparacrista connecting as a straight centrocrista which parallels the preparacrista. Lacking preprotocrista, postprotocrista, protoconule, metaconule, stylar shelf or stylar cusps antcrior to St E. Buccal flank of crown forming continuous slope from paracone and metacone to lowest buccal edge of the crown. Protocone small.

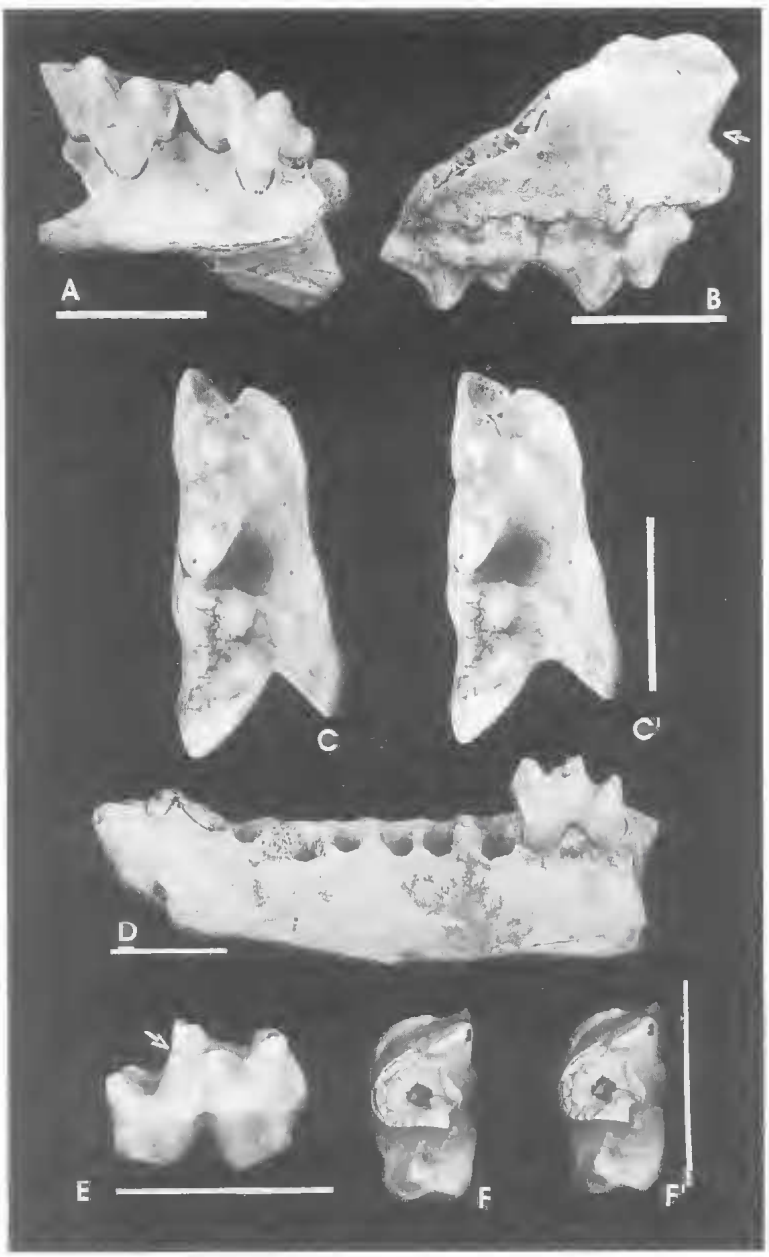

FIG. 1. *Wabulacinus ridei.* A = QMF16851 (M^1 and M^2) lingual view. B = QMF16851 (M^1 and M^2) buccal view with infraorbital foramen arrowed. C and C' = QMF16851 stereo occlusal views. D = QMF16852 (P_2 and M_3) buccal view. E = QMF16852 (M_3) lingual view showing small metaconid (arrowed). F and F' = QMF16852 stereo occlusal view.

M^2 similar to M^1 except : St E minute. Stylar shelf region high, of many tiny indistinct cusps and crests, especially on the more posterior half of the crown. Postmetacrista longest crest on the crown, followed in declining length by preparacrista, postprotocrista, preprotocrista, postparacrista and premetacrista. Postparacrista and premetacrista forming a wide angled centrocrista. Postmetacrista leaving metacone almost parallel to the premetacrista, curving buccally. Preparacrista straight, connecting to the postpara-

crista at approximately 90° and oblique to the tooth row. No St B present. Trigon basin wider than on M^1. Lingual flank of trigon basin 'V'-shaped with a distinct ridge running vertically down its centre. The preprotocrista and postprotocrista prominent with a minute protoconule and metaconule. Ectoflexus on the buccal surface of this tooth slightly developed. Anterior cingulum terminating anterior to base of the paracone, lacking a notch.

Mental foramen under the anterior root of P_2. Alveoli for P_{1-3}, M_{1-2} and the anterior root of M_4. M_3 only molar present. Symphysis beginning adjacent to the anterior root of P_3. No diastemata between alveoli. All alveoli pairs orientated parallel to the tooth row except P_1 oblique, indicating some crowding of P_1 against the canine. Alveoli size indicating relative lengths of $P_3 > P_2 > P_1$, $M_3 = M_2 > M_1$.

M_3 with cusps in decreasing height paraconid, metaconid, hypoconulid, hypoconid. All cusps prominent except minute metaconid; entoconid and related crests absent. Protocristid longest crest, followed (in decreasing length) by the posthypocristid and cristid obliqua. Remains of the metacristid connect to the small metaconid. Small talonid basin open on the lingual side. Hypoconid almost medial to the trigonid basin. Posthypocristid and cristid obliqua orientated oblique to the dentary, meeting at the hypoconid at right angles. Anterior cingulum continuing buccally past the anterobuccal corner of tooth, with wide notch. Posterior cingulum poorly developed, a small bulge in the enamel.

Ngamalacinus gen. nov.

TYPE SPECIES. *Ngamalacinus timmulvaneyi* et sp. nov.

ETYMOLOGY. Wanyii *Ngamala*, died out; *Greek kynos*, dog. Masculine.

DIAGNOSIS. Moderately specialised among thylacinids in the reduced conules, reduced stylar shelf, anteroposteriorly elongated molars. Retaining small St B and D, metaconid, entoconid and hypoconulid.

COMPARISON. *Ngamalacinus* differs from *N. dicksoni* in its larger size, reduced metaconules and protoconules, reduction of St D particularly on M^2.

Ngamalacinus differs from *W. ridei* and *Thylacinus* in its: smaller size; narrower angle of crests at the paracone, metacone and protocone; narrower angle of centrocrista; less reduced stylar shelf with retention of prominent St B, St D and stylar shelf crests on M^1 and M^2; less reduced talon basin, particularly on M^1; less anteroposterior elongation of the molars and associated crest lengths; larger talonids; and larger metaconid (larger than the paraconid) and with a distinct metacristid.

Ngamalacinus further differs from *W. ridei* in the more posterior position of the infraorbital foramen, presence of an entoconid on the lower molars and smaller hypoconulid.

Ngamalacinus timmulvaneyi sp. nov.
(Figs 2, 3)

ETYMOLOGY. For Tim Mulvaney, a long-time supporter of research at Riversleigh.

MATERIAL. Holotype QMF16853 right dentary with M_{1-4} (Fig. 2) from early Miocene (System B) Inabeyance Site, Godthelp Hill, Riversleigh. Paratypes QMF30300 left maxillary with P^2-M^3 (Fig. 3A-C), from early Miocene (System B) Camel Sputum Site, Godthelp Hill. Referred specimen QMF16855, right M^2 (Fig. 3D), from the type locality.

DIAGNOSIS. As for genus.

DESCRIPTION. All articulating surfaces of dentary broken. Coronoid process rising from the ramus at approximately 120°. All four molars and the posterior alveolus of P^3 present. No diastemata between these teeth. Degree of eruption of M_4 indicating a juvenile.

Protoconid of M_1 tallest cusp, followed (in decreasing height) by metaconid, paraconid, hypoconid, hypoconulid and entoconid. All cusps distinct, with crests. Paracristid longest crest on crown followed (in decreasing length) by posthypocristid, metacristid, cristid obliqua, pre-, postentocristid. Anterior cingulum with a very small notch. Paracristid almost straight with a very wide angle connecting the paraconid and protoconid. Talonid basin entirely enclosed by crests, large and deeply concave to central point. Hypoconid more buccally positioned than protoconid. Cristid obliqua continuing up the posterior wall of the protoconid. Posterior cingulum distinct, uniform in thickness to the base of the crown, with a slight notch formed between it and the hypoconulid.

M_2 same as M_1 except: Metaconid relatively large, distinct, taller than the paraconid. All cristids higher and distinct. Anterior cingulum broader and the notch more distinct. Angle at crests on the protoconid approximately 100–110°.

Paracristid and metacristid longer. Metacristid straight; paracristid changing orientation at the valley between the paraconid and protoconid.

M_3 same as M_2 except: the anterior half of the crown thicker than the posterior because of the more lingual position of the paraconid and metaconid. Paracristid and metacristid elongated. Hypoconulid and entoconid slightly more to posterior, with entoconid slightly smaller than on M_2. Posthypocristid bending posteriorly to connect to the posteriorly positioned hypoconulid. Paracristid proportionally longer than on M_2.

M_4 same as M_3 except: Talonid basin reduced, well defined and enclosed by crests. Entoconid minute; hypoconid small; hypoconulid highest cusp on talonid. Small posterior cingulum present.

No obvious sutural boundaries on the maxilla except a posterior suture that may have connected to either the jugal or the lachrymal. Maxilla indicating that the canine was large, its root extending deeply into the maxilla. Infraorbital foramen above M_2. The region immediately posterior to the infraorbital foramen damaged but a depression in the maxilla here and sutural boundaries of the jugal indicate that the jugal is likely to have contacted the external opening of the infraorbital canal. Maxilla with large extension projecting back towards and contributing to the zygomatic arch. No maxillary palatal vacuities in the region of the premolars.

Small diastemata between the upper premolars. P^2 triangular in lateral view with both an anterior and posterior cusp, with a crest from the major central cusp to the posterior cusp and a less well defined crest anteriorly to the smaller anterior cusp, with posterior region wider than the anterior, with ridges extending along both sides (lingual and buccal) of the posterior cusp. P^3 larger than P^2 and similar except for: anterior and posterior cusps relatively larger, anterior cusp with ridges off the lingual and buccal sides, posterior crest from the major cusp more prominent but not straight, posterior half of tooth relatively wider with enlarged crests bordering the posterolingual and posterobuccal edges of the crown, with an additional posterobuccal cusp.

M^1 damaged, with anterior cingulum, a large St D larger than the distinct St B, a stylar crest running posteriorly from St D to the metastylar corner, talon broad with a possible protoconule, postmetacrista long and straight, crests at the paracone at approximately 90°, preparacrista connecting to St B, almost perpendicular to the tooth row.

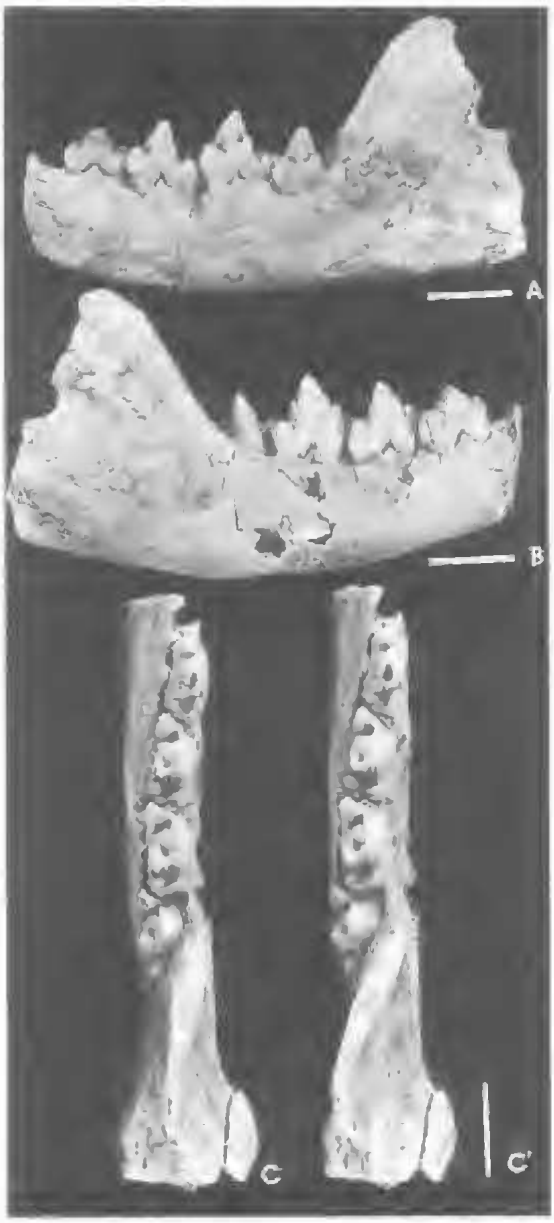

FIG. 2. *Ngamalacinus timmulvaneyi* lower dentition. A = QMF16853 (dentary with M_{1-5}) lingual view. B = QMF16853 buccal view. C and C^1 = QMF16853

M^2 same as M^1 with: in occlusal view posterolingual dimension longest followed by buccal length and anterior width. Anterior cingulum not notched in QMF16855 but is in QMF30300, cingulum terminating at the anterior face of the base of the paracone without connecting to the talon basin. No posterior cingulum. Metacone highest cusp on the crown, followed (in

decreasing height) by: paracone, St B, metastylar cusp(s) and protocone. Postmetacrista longest crest on the crown, followed by the preparacrista, premetacrista, postprotocrista, preprotocrista and postparacrista. All crests relatively straight. Enamel surface slightly raised about the protoconule. Metaconule not present as a distinct cusp. Slightly raised postprotocrista connecting the protocone to the metacone base where a sharp crest runs up the lingual surface of the metacone. A less distinct ridge running down the lingual side of the paracone and protocone. Slight ectoflexus at the buccal side of the crown due to bulging of enamel around St B. St E a raised part of the stylar crest. Between St E and B are minute cusps on QMF16855 but St D is more distinct on QMF30300. One crest connecting the metastylar cusp(s) to the posterolingual corner of the crown. Talon basin large with a broad, flat base. Preprotocrista and postprotocrista relatively low. Centrocrista at approximately 100°.

M^3 same as M^2 except: Ectoflexus stronger and all stylar cusps reduced to cuspules. Stylar crest not continuous along the lingual edge of the crown. St B largest stylar cusp. Anterior cingulum with less distinct notch than in M^2 of QMF30300. Preparacrista and postmetacrista longer; paracone relatively larger but smaller than metacone. Paracone more lingually located. Centrocrista at approximately 90°; postparacrista strongly curved. Talon narrower. Protoconule and metaconule with ridges connecting to the lingual face of the paracone and metacone respectively.

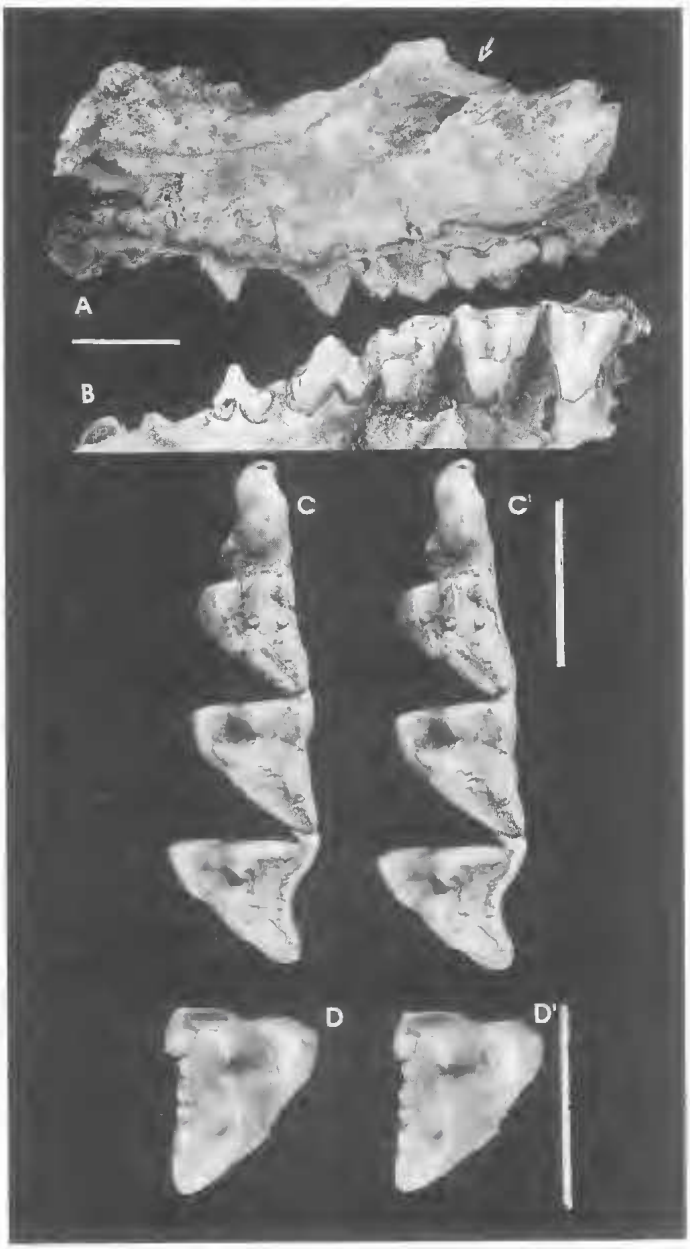

FIG. 3. *Ngamalacinus timmulvaneyi* upper dentition. A = QMF30300 maxillary fragment with P^2-M^3 and showing infraorbital foramen (arrowed). B and B^1 = QMF30300 stereo occlusal view of P^3 and molars. C = QMF30300 lingual view. D and D^1 = QMF16855 (M^2) stereo occlusal views.

THYLACINID PHYLOGENY

Ngamalacinus timmulvaneyi and *W. ridei* do not share any apomorphies that are not also found in *Thylacinus*. These, therefore, cannot be considered to represent members of the same genus.

Wabulacinus ridei and *Ng. timmulvaneyi* have combinations of features that place them between plesiomorphic *N. dicksoni* and apomorphic *Thylacinus* but do not form an independent dichotomy (Fig. 4). Neither species can be placed in a known genus because: neither shares any

TABLE 1. Characters and states among thylacines.

1. Infraorbital foramen: 0. not bound by jugal. 1. bound by jugal.

2. Centrocrista. 1. angled. 2. straight (as indicated by M^1).

3. Preparacrista on M^1. 1. angled almost perpendicular to the tooth row axis. 2. wider angle than state 1. 3. straight.

4. Angle of crests at paracone and metacone. 1. wider than on plesiomorphic dasyurids. 2. further widened.

5. Entoconid. 1. small. 2. minute. a. either absent or posteriorly positioned and combined with the hypoconulid.

6. Hypoconulid size. 0. large. 1. reduced. 2. minute.

7. Stylar shelf size. 1. crests and cusps present but reduced compared to plesiomorphic dasyurids. 2. reduction in size of some cusps and crests. 3. further loss of cusps and crests (mostly absent on M^1). 4. complete loss on crests, only a single small cusp present on the posterior of the crown.

8. Anterior cingulum. 0. complete on M^1. 1. incomplete on M^1.

9. Metaconule and protoconule. 0. present and large. 1. present and reduced. 2. further reduced or absent.

10. Metaconid size. 1. reduced compared to plesiomorphic dasyurids. 2. small. 3. absent but retension of crest arrangement in posterior molars. 4. complete absence of cusp and associated crests.

11. Talonid basin size. 0. unreduced. 1. reduced by lingual placement of hypoconid. 2. further reduction.

12. Talon size. 1. reduction of talon width compared to plesiomorphic dasyurids with associated lengthening. 2. loss of metaconid and further widening of the crests

13. Diastemata and size of M_4. 0. no diastemata in premolar region, M_4 shorter than M_3. 1. diastemata and M_4 equal in length to M_3. 2. diastemata and M_4 is longer than M_3.

TABLE 2. Character state distribution among thylacines. (a = either 0 or autapomorphic combination of entoconid and hypoconulid, ? = unknown state).

Dasyurids	00000 00000 000
Nimbacinus dicksoni	11111 11001 010
Ngamalacinus timmulvaneyi	11111 12011 010
Wabulacinus ridei	0232a 03112 12?
Thylacinus macknessi	?2222 24023 221
Thylacinus potens	12222 24024 222
Thylacinus cynocephalus	12222 24124 222

apomorphy with *N. dicksoni* that is not also shared with *Thylacinus*; to include either in *Thylacinus* would expand it beyond any other dasyuromorphian genus. *Wabulacinus ridei* shows character conflict in the plesiomorphic nature of the infraorbital foramen which is more plesiomorphic than in *N. dicksoni* and *Ng. timmulvaneyi*. This character may have undergone reversal in *W. ridei*.

The single most parsimonious tree of thylacinid relationships was found using an Exhaustive Search PAUP 3.1 (Swofford, 1993) with 13 ordered characters (Tables 1 & 2) using pleisomorphic dasyurids as the outgroup. Each taxon represents the sister species of all thylacines immediately to its right. In general, the more specialised carnivores are located on the right.

Wabulacinus ridei and *Ng. timmulvaneyi* are more plesiomorphic than *Thylacinus* in the larger size of the metaconid (small on *W. ridei* and much larger on *Ng. timmulvaneyi*) and the lack of expansion of the premaxillary region. Both species (and particularly *W. ridei*) are more specialised than *N. dicksoni* in the reduction of the stylar shelf and the metaconule and protoconule, talon basin and degree of ectoflexus on M^3.

WABULACINUS RIDEI. Features that are more apomorphic than in *N. dicksoni* and are synapomorphic with *Thylacinus* are: the straight centrocrista; the widened angle of the preparacrista relative to the postparacrista, particularly on the M^1 where this crest is parallel with the anteroposterior dimension of the tooth; an increase in the size of the angle formed by crests at the paracone and metacone, thereby increasing overall tooth length; further reduction in size of the stylar cusps than that seen in either *Ng. timmulvaneyi* and *N. dicksoni;* reduction in size of the entoconid; reduction of the metaconid to a minute cusp; reduction in size of the talonid basin by the more lingual position of the hypoconid; and reduction in size of the talon basin.

Wabulacinus ridei exhibits some autapomorphies not seen in any other thylacinid, some of which are considered specialisations beyond that of *T. cynocephalus*. The preparacrista on M^1 of *W. ridei* is parallel with the tooth row and the centrocrista. The preparacristae on *N. dicksoni* and *Ng. timmulvaneyi* show the plesiomorphic state similar to most dasyurids in which it lies almost perpendicular to the tooth row and forms almost a 90° angle with respect to the postparacrista. The morphocline otherwise shown in thylacines from *N. dicksoni* through to *T. cynocephalus* is a widening of the angle at which these crests meet (Fig. 5). This elongates the tooth in an anteroposterior direction and pro-

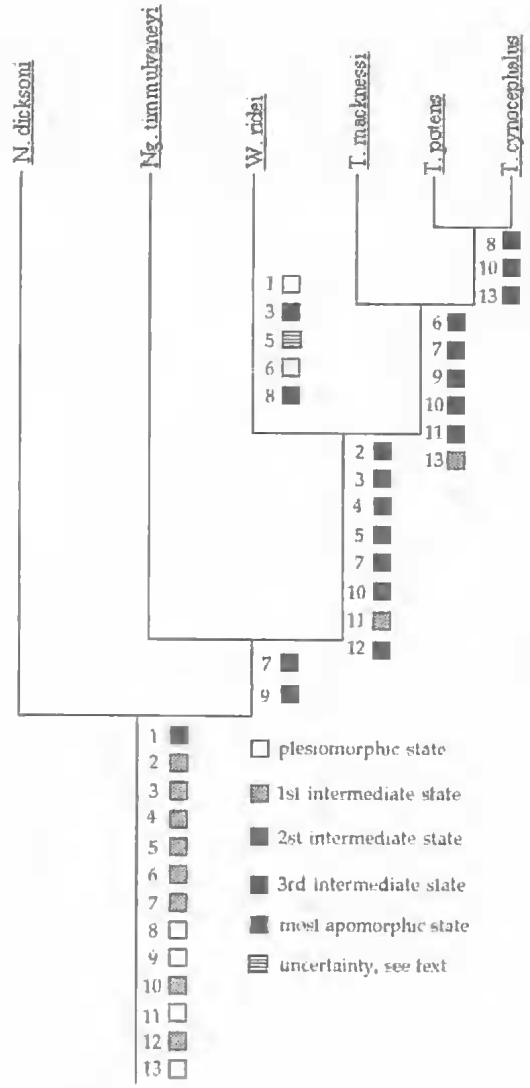

FIG. 4. Cladogram of thylacines showing character state changes. Cladogram is the single most parsimonious tree of 32 steps (CI = 0.906, HI = 0.094, RI = 0.917, RC = 0.831). Striped box = unknown state of either plesiomorphic or highly derived. For characters and their distribution see Tables 1 & 2.

duces an enlarged longitudinal blade formed from the postmetacrista, centrocrista and preparacrista. Only on M^1 of *W. ridei* does the preparacrista lie parallel to the tooth row, a condition more derived than that in any other thylacine. The talon basin on the M^1 of *W. ridei* is also more derived in its degree of reduction than that of *T. macknessi* but is similar to the condition in *T. cynocephalus*.

The anterior cingulum on M^1 of *W. ridei* is reduced compared to that of *N. dicksoni* (it is unknown in *Ng. timmulvaneyi*). In *W. ridei* it is incomplete while in *N. dicksoni* it continues lingually to join the talon basin. This feature is more plesiomorphic than in *T. cynocephalus* where the cingulum is lost, but more specialised than in *T. macknessi* where a complete cingulum is retained. In addition, the anterior portion of M^1 of *W. ridei* is unique in that the anterior root lies much further forward under the crown than in other thylacines.

Another trend in thylacines is for the entoconid to become reduced. Only in *W. ridei* is this cusp completely lost.

Wabulacinus ridei is autapomorphic within the family in having an enlarged hypoconulid. In other thylacines the hypoconulid shows reduction (e.g., in *N. dicksoni*, *T. cynocephalus*) and may also move posteriorly (e.g., in *T. macknessi*). This enlarged cusp in *W. ridei* may be compensate for loss of the entoconid, or alternatively, it may represent a combination of the hypoconulid and a more posteriorly placed entoconid.

A feature previously used to distinguish thylacines from dasyurids is the posterior position of the infraorbital foramen posteriorly delimited by the jugal (Muirhead & Archer, 1990). It is known in *T. cynocephalus*, *T. potens*, *Ng. timmulvaneyi* (Fig. 3A) and *N. dicksoni*. *Wabulacinus ridei* has the infraorbital foramen anterior to M^1 and well distant from the jugal (Fig. 1B). This position is similar to dasyurids in which it most frequently occurs above M^1/M^2 (e.g., in *Dasyurus* and *Antechinus*). The anterior position of this foramen in these dasyurids indicates that posterior placement near the jugal in most thylacines is apomorphic (Archer, 1976). The anterior placement of the jugal in *W. ridei* is therefore plesiomorphic relative to other thylacinids.

Wabulacinus ridei is plesiomorphic in many respects to *Thylacinus* excluding it from *Thylacinus*. *W. ridei* has a number of features unique among thylacinids placing it outside the range of variation within *Thylacinus*.

NGAMALACINUS TIMMULVANEYI. This species shares with *W. ridei* and *Thylacinus* the apomorphic reduction in the stylar shelf compared to *N. dicksoni* (Fig. 4). This includes reduction in size of St D of M^2. On QMF16855, St D is further reduced and replaced by a number of minute cusps that border the stylar shelf. On other

molars, size of the stylar shelf is comparable to that in *N. dicksoni*.

The protoconules and metaconules of *W. ridei* are apomorphically reduced compared to those of *N. dicksoni*. The talon basin is also slightly more reduced than that of *N. dicksoni*. This species further differs from *N. dicksoni* in the less extreme ectoflexus, an apomorphic feature. These specialisations of *Ng. timmulvaneyi* compared to *N. dicksoni* are less marked than the degree of specialisation of these same features in *W. ridei* and *Thylacinus*. *Ngamalacinus timmulvaneyi* and *N. dicksoni* share several plesiomorphies and, in terms of overall similarity, *Ng. timmulvaneyi* is much closer to *N. dicksoni* than to any other thylacinid (Fig. 4). These two species do not share any apomorphy not also found in other thylacines.

PALAEOECOLOGY OF RIVERSLEIGH THYLACINIDS

Thylacinids described from the Riversleigh assemblages are *N. dicksoni*, *Ng. timmulvaneyi*, *W. ridei* and *T. macknessi*. This diversity raises questions about niche diversification. Although only one thylacine appears to have been present at any one time in late Miocene (Alcoota, *T. potens*), Pliocene (Awe & Chinchilla, *T. cynocephalus*) and Quaternary (many assemblages, *T. cynocephalus*) local faunas of Australia and New Guinea (Archer, 1982; Dawson, 1982), prior to the late Miocene, available resources enabled the "thylacine niche" to be more finely divided. Part of the explanation may be found in the apparent absence from the Riversleigh local faunas of any large dasyurids as specialised for carnivory as the late Cainozoic species of *Glaucodon*, *Sarcophilus* and *Dasyurus*. Presence of large carnivorous dasyurids appears inversely correlated with thylacinid diversity. The subsequent rise of these dasyurines may, therefore, have accompanied late Miocene decline in thylacinid diversity.

Although there is a greater diversity of thylacines in the Oligo-Miocene Riversleigh deposits than later, a wider range of large carnivores was also present in these Riversleigh local faunas. For example in single local faunas, there were often 3 crocodilians (P. Willis, pers. comm.), at least 2 large snakes (madtsoiids and pythonids; J. Scanlon, pers. comm.), 2 lineages of thylacoleonids (*Wakaleo* and a genus similar to *Priscileo*; Archer et al., 1989), a possibly carnivorous kangaroo (Archer & Flannery, 1985; Wroe & Archer, 1995; Wroe, 1996) and an unknown number of raptorial birds (Boles, pers. comm.; Archer et al., 1994). Hence it is probable that the relatively high diversity of Riversleigh thylacines reflects an overall higher biotic diversity in the rainforests of the Riversleigh region.

Camel Sputum is the only Riversleigh site to have produced more than one thylacine: *Ng. timmulvaneyi* and *W. ridei*. These taxa are very similar in size. The maxilla of *Ng. timmulvaneyi* recovered from Camel Sputum Site differs from the maxilla of *W. ridei* in the position of the infraorbital foramen (in *Ng. timmulvaneyi* it typically lies above M^2 and was probably bounded by the jugal while in *W. ridei* it lies anterior to M^1) and the more plesiomorphic structure of the molars in *Ng. timmulvaneyi*. These differences cannot be accounted for by intraspecific variation and the specimens clearly represent two different species.

It is not clear how many of Riversleigh's thylacines co-existed. While 2 are present in the Camel Sputum assemblage, the more generalised *N. dicksoni* may have been present throughout the Oligo-Miocene (Systems A to C; Muirhead & Archer, 1990). *Thylacinus macknessi* in Systems B and C (Muirhead, 1992) suggests that by the early to middle Miocene, all 4 genera co-existed at Riversleigh. By late Miocene Alcoota time, one lineage is known: *T. potens*.

In late Cainozoic deposits from other areas of Australia (i.e., cave assemblages in eastern, southern and western Australia; Ride, 1964; Archer, 1974, 1982; Dawson, 1982), thylacinid remains are common. Sites where thylacinid remains are abundant (e.g., Thylacine Hole on the Western Australian Nullarbor; Lowry, 1972) may be interpreted to represent lairs or traps where carnivores were preferentially attracted, perhaps by the presence of other animals. In the Riversleigh deposits, most of which appear to have accumulated in shallow pools within rainforest environments (Archer et al., 1989; Archer et al., 1994), thylacinid remains are relatively rare and therefore may more fairly represent natural frequencies.

THYLACINID DIAGNOSIS AND MORPHOLOGICAL TRENDS

Thylacinids differ from dasyurids and other polyprotodont marsupials by having, in combination, the following features. The premetacrista and postparacrista join as a centrocrista. The angle formed by these crests is straight or almost straight in occlusal view in at least M^2 of the

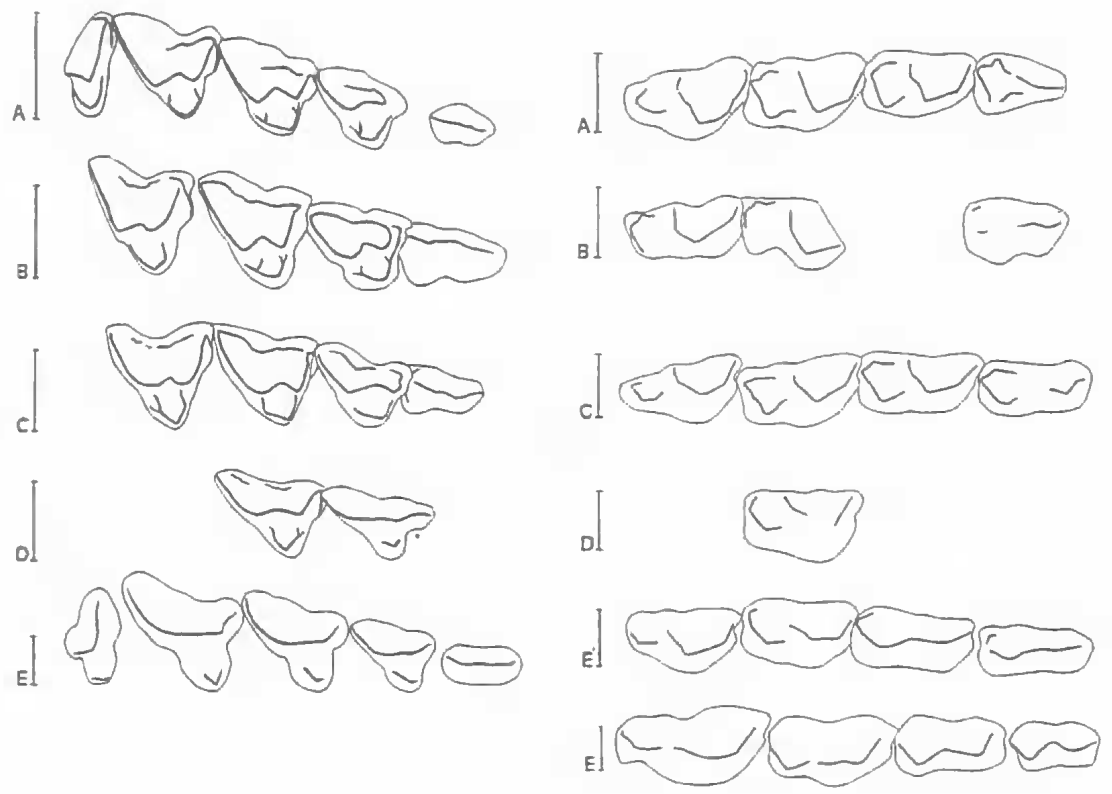

FIG. 5. Upper and lower dentitions of all known thylacine genera showing crest orientation compared to a dasyurid. A=*Dasyurus*. B=*Nimbacinus dicksoni* (P8695-92) C=*Ngamalacinus timmulvaneyi*. D=*Wabulacinus ridei*. E^1=*Thylacinus macknessi* E=*Thylacinus cynocephalus*. Upper dentitions include P^3 where known. Scales = 0.5mm.

upper dentition. The eristid obliqua continues up the posterior flank of the protoconid from the talonid region rather than terminating at the base of the protoconid. This functions in elongating this crest and becomes more prominent as the metaconid is reduced (e.g., in *Thylacinus*). The stylar cusps are reduced. This occurs most prominently on M^3 but also occurs to varying degrees on more anterior molars. The size of the metaconid is reduced on all lower molars. This reduction is correlated with the more posterior placement of the metaconid relative to the protoconid, functioning in widening the angle of crests at the protoconid and enlarging the trigonid basin. Reduction of the metaconid is also found to progress in degree from the more reduced condition on anterior molars to posterior molars (Muirhead & Gillespie, 1995). The size of the talonid basin is reduced because of the more lingual position of the hypoconid. This cusp occupies much of the surface of the talonid basin such that no flat surfaces occur on the basin floor.

Structural morphoclines of the family (apparent in more specialised forms) include the following. There is an increase in the angles formed by crests of the paracone and metacone, increasing the length of the postmetacrista. More anteroposterior orientation of the preparacrista. The loss of extreme ectoflexus particularly in M^3 (related to the overall elongation of the teeth). A reduction in size of the protoconule and metaconule as well as the entire talon basin and reduction in size of the stylar shelf. All of these features of the upper dentition increase the anteroposterior length of the molars with the entire tooth row acting as a system of anteroposteriorly orientated blades (Fig. 5). These are typical specialisations in mammalian carnivores.

In the lower molars, the trends are for complete loss of the metaconid and opening of the trigonid

basin. Here, like the upper molars, the lower molar crests become orientated anteroposteriorly (Fig. 5). The paracristid becomes the anterior crest with the elongated cristid obliqua functioning as the posterior crest (the postprotocrista) (Muirhead and Gillespie, 1995). The lingual side of the talonid is also reduced through reduction of the entoconid.

Only in *Thylacinus* is the snout elongated by both diastemata between the canine and premolars and elongation of M4 (such that it is longer than preceding molars). Extreme posterior placement of the infraorbital foramen and partial enclosure by the jugal is also a possible synapomorphy of *Thylacinus* related to snout elongation.

All thylacinids plesiomorphically retain the paraconid on M_1, remnants of posterior and anterior cingula on the lower molars and posterior increase in size from P_1 to P_3.

Variation among thylacinids that does not appear to follow these 'carnivorous trends' includes position of the infraorbital foramen which, plesiomorphically and unlike all other known thylacinids, is more anteriorly positioned in *W. ridei* above P^3.

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APPENDIX

All measurements are actual distance between cusps except those with '(horiz)' for which measurements were made from a horizontal plane above the cusps (occlusal view).

Wabulacinus ridei dentition (mm)

QMF16851 QMF16852	M^1	M^2	M_3
Para-meta	3.56	3.59	5.06
Meta-proto	4.20	5.01	-
Proto-para	2.64	3.53	-
Anterior/width	5.20	6.60	5.20
Buccal/length	9.00	8.92	9.40
Posterolingual /uppers	7.37	8.36	-
para-meta (horiz)	2.90	3.40	4.36
meta-proto (horiz)	2.35	3.55	-
proto-para (horiz)	2.35	2.85	-
hypo-hypoconulid	-	-	-
hyp-ento	-	-	1.81'

Ngamalacinus timmulvaneyi upper dentition (mm)

QMF30300 QMF16855	P^2	P^3	M^1	M^2	M^2	M^3
Para-meta			3.64	3.66	3.34	3.03
Meta-proto			2.86	3.36	3.65	5.00
Proto-para			3.77	5.14	5.02	5.52
Anterior/width	2.25	4.26	4.90	7.68	7.20	8.25
Buccal/length	5.56	7.92	8.11	9.10	8.76	8.17
Posterolingu /uppers			8.15	10.29	9.30	10.27
para-meta (horiz)			3.30	3.42	3.31	2.80
meta-proto (horiz)			2.28	3.05	2.84	3.04
proto-para (horiz)			3.34	3.25	3.35	3.20

Ngamalacinus timmulvaneyi lower dentition (mm)

QMF16853	M_1	M_2	M_3	M_4
Para-meta	3.56	3.97	4.53	4.37
Meta-proto	-	3.09	3.35	3.47
Proto-para	-	4.11	4.92	4.79
Anterior/width	3.34	4.21	4.25	4.78
Buccal/length	7.69	8.37	8.70	8.24
para-meta (horiz)	3.62	3.98	4.50	4.27
meta-proto (horiz)	-	2.51	2.64	2.43
proto-para (horiz)	-	3.88	3.89	4.03
hypo-hypoconulid	2.05	2.26	2.10	1.34
hyp-ento	0.76	1.08	1.13	0.90